ELSEVIER

Forest Ecology and Management 109 (1998) 51–56

Forest Ecology and Management

Impacts of live canopy pruning on the chemical constituents of Douglas-fir vascular tissues: implications for black bear tree selection

Bruce A. Kimball[a,*], Dale L. Nolte[b], Doreen L. Griffin[a], Steve M. Dutton[c], Steve Ferguson[d]

[a] USDA/APHIS/NWRC 3350 Eastbrook Drive, Ft. Collins, CO 80225, USA
[b] USDA/APHIS/NWRC 9701 Blomberg Street SW, Olympia, WA 98512, USA
[c] Oregon Department of Forestry, 4907 Third Street, Tillamook, OR 97141, USA
[d] Oregon Department of Forestry, Route 1, Box 950, Astoria, OR 97103, USA

Received 30 September 1997

Abstract

The impact of live canopy pruning on the carbohydrate and terpene content of vascular tissue was investigated in the lower bole of Douglas-fir (*Pseudotsuga menziesii*). Cambial zone vascular tissue samples were collected from pruned and unpruned trees in the lower bole and within the live canopy. Current year's radial growth was estimated from the mass of vascular tissue removed from the 800 cm^2 sample area. Chemical analyses were conducted to determine the concentration of carbohydrates and terpenes in the samples. Results indicated that two years following treatment, pruning resulted in reduced growth and decreased carbohydrate content of the vascular tissue. Pruning had no effect on the terpene concentration of the vascular tissue. The impact of pruning on the foraging selection of black bears (*Ursus americanus*) was evaluated by surveying bear damaged trees in a 50 acre stand of pruned and unpruned timber. Odds ratios indicate that black bears were four times more likely to forage unpruned Douglas-fir than pruned Douglas-fir. Tree selection may be explained in part to the higher availability of carbohydrates in the unpruned tree with respect to the pruned tree. © 1998 Elsevier Science B.V.

Keywords: Forage preference; Forest management; Pruning; Silviculture; *Ursus americanus*

1. Introduction

Black bear (*Ursus americanus*) foraging of coniferous vascular tissues is detrimental to the health and economic value of timber stands, in addition to impeding reforestation efforts. Bears forage on the cambial zone vascular tissues in the lower bole by removing or 'peeling' the bark with their claws and scraping the vascular tissue with their incisors. Complete girdling from peeling is lethal, while partial girdling leads to lower growth rates, insect infestation, and/or disease (Kanaskie et al., 1990). An individual bear can peel the bark of 50–70 trees per day (Schmidt and Gourley, 1992).

Many conifer species are peeled by bears. However, preference for Douglas-fir (*Pseudotsuga menziesii*) is commonly reported (Barnes and Engeman, 1995).

*Corresponding author. Fax: 001 970 225 1854; e-mail: a347bkimball@attmail.com

0378-1127/98/$19.00
PII S0378-1127(98)00260-6

Preference for trees in thinned stands versus higher density stands is well known (Schmidt and Gourley, 1992; Kanaskie et al., 1990; Mason and Adams, 1989).

Mammalian forage selection is largely driven by the feedbacks associated with the chemical constituents of the forage item (Provenza et al., 1992). For example, carbohydrates and terpenes have recently been shown to impact black bear foraging preferences (Kimball et al., in press). Bears select forage in a manner that maximizes carbohydrate intake while minimizing the intake of terpenes. We anticipated that live canopy pruning would significantly affect these chemical constituents of vascular tissue.

Pruning is typically performed to increase wood quality by affecting stem form (less taper), producing knot-free wood, and increasing wood density (O'Hara, 1991). A recent survey of landowners in the Pacific Northwest indicated that approximately 4% of lands reforested to Douglas-fir in the past ten years have been or will be pruned (SMC, 1997). This study was designed to investigate the impacts of pruning on the carbohydrate and terpene concentrations of Douglas-fir vascular tissue. We also hypothesized that these changes would impact black bear tree selection.

2. Methods

2.1. Study sites

Vascular tissues samples were collected at three Oregon Department of Forestry (ODF) sites in the coast range of Northwestern Oregon. Samples were collected on May 22–23, 1996; at Big Spruce Area I and Big Spruce Area II, located near Necanium Junction, Oregon (Table 1). Samples were collected on May 31, 1996; at the Wage Road Number 2 site, located near Jewell, Oregon. Black bear damage was surveyed on May 28, 1997; at the God's Valley Number 3 site, located near Nehalem, Oregon.

2.2. Pruning treatments

Live canopy or 'green' pruning was performed by removing all live and dead whorls between the ground and 5 m with a pruning saw. This resulted in the removal of approximately 40% of the live canopy. A 50% pruning regime was applied such that every other tree was pruned. Only Douglas-fir trees were pruned at the Big Spruce and Wage Road sites, although Western hemlock (*Tsuga heterophylla*) was also present. Pruning treatments were applied 2 years prior to vascular tissue sampling (Table 1).

A similar pruning treatment was applied at the God's Valley Number 3 site except that both Douglas-fir and Western hemlock were subjected to the pruning regime. Trees with existing bear damage were marked at the time of treatment by painting the damaged area with tree marking paint. Trees were pruned 4 years prior to the damage survey (Table 1).

2.3. Vascular tissue collection

An 80 cm (vertical) × 10 cm (horizontal) patch of bark was removed from the east side of the first randomly selected pruned tree by cutting the bark with forged metal tools resembling meat cleavers. This lower bole height sample was obtained at 1 m by scraping the vascular tissue (phloem and xylem oleoresin located immediately underneath the cork cambium) into a tared plastic freezer bag with a laboratory spatula. The freezer bag and contents were immediately frozen in liquid nitrogen and maintained on dry ice until transported to a laboratory freezer.

The pruned tree was then felled by chainsaw and the height of the first whorl of live branches was mea-

Table 1
Sites located in Northwestern Oregon used to study the effects of pruning on vascular tissue chemistry and black bear foraging preference.

Site	Legal	Size	Year Planted	Year Thinned	Tree Density[a]	Year Pruned	Year Sampled
Big Spruce Area I	S.10 and 15, T.4N, R.8W	10.5 ha	1980	1991	490	1994	1996
Big Spruce Area II	S.10, T.4N, R.8W	7.3 ha	1980	1991	480	1994	1996
Wage Road Number 2	S.18 and 19, T.5N, R.6W	13.8 ha	1974	1987	420	1994	1996
God's Valley Number 3	$E^{1/2}$, S.4, T.3N, R.9W	21.4 ha	1974	1986	420	1993	1997

[a] Trees per hectare after thinning treatment.

sured. The mid bole sample was collected at the height of the first live whorl as described above. The upper bole sample was similarly obtained at a point in the bole half-way between the mid bole sample and the top of the tree. The sample heights for the mid and upper bole samples were recorded.

An adjacent unpruned tree of similar diameter and height was then selected for sampling. The lower bole sample was also collected at a height of 1 m. After the tree was felled, the mid and upper bole samples were collected at identical heights in the bole as the adjacent pruned tree. Eight pruned and eight unpruned trees were similarly sampled at each site.

2.4. *Chemical analyses*

Samples were maintained frozen and the mass of the bag and contents was determined. Each vascular tissue sample was homogenized in the sample bag by striking with a mallet. The homogenized sample was then divided into two equal portions. One portion was maintained frozen until extracted with ethyl acetate and analyzed for terpene content by gas chromatography according to the method of Kimball et al. (1995). The hydrocarbon monoterpene, oxygenated monoterpene, and sesquiterpene compounds present in the extracts were individually quantified.

The other portion of the sample was lyophilized and extracted with 50% ethanol in water. The extract was analyzed for carbohydrates by anion exchange chromatography (Rocklin and Pohl, 1983). Glucose, fructose, and sucrose were quantified in the extracts. Detailed description of the chemical analysis of vascular tissue can be found in Kimball et al., in press.

2.5. *Survey data collection*

Five-man crews walked 5 linear transects through the 21.4 ha God's Valley Number 3 site. Transects were approximately 15 m wide which was distinguished by maintaining a spacing of four trees. Each conifer falling in the transect path was inspected for the following: tree species, treatment (pruned or unpruned), presence of bear damage inflicted since the pruning treatment (yes or no), and presence of pre-treatment damage (damage identified with tree marking paint).

2.6. *Statistical analyses*

Chemical data were analyzed as blocked two-factor analyses of variance (ANOVA) with two levels of treatment (pruned and unpruned) and three bole heights (lower, mid, and upper bole). The three sites were the blocks. Responses were vascular tissue mass, total hydrocarbon monoterpenes, total oxygenated monoterpenes, total sesquiterpenes, and major carbohydrates. Trees were not considered to be replicates in this design. Rather, mean values of the responses were calculated from the eight trees for each treatment and bole height combination.

Contingency tables generated from the bear damage survey data were analyzed with chi-square tests of independence. Contingency tables of Douglas-fir and Western hemlock pre-treatment damage data were created to determine if pruning treatments were applied independently of existing damage. Contingency tables were then produced with the post-treatment damage data for both Douglas-fir and Western hemlock. Odds ratios were calculated from the post-treatment damage data. Statistical analyses were designed according to Ott (1993) and performed using SAS (SAS, 1990).

3. Results

Chemical data were analyzed as two-factor analyses following the observation that no treatment×bole height interactions existed for any response. Pruning resulted in decreased vascular tissue mass as well as decreased vascular tissue carbohydrate concentration (Table 2). Pruning increased the vascular tissue concentration of the sesquiterpenes from 0.15 to 0.37 ppm.

Bole height effects were significant for all responses except major carbohydrates (Table 2). Vascular tissue concentrations of the terpenes were highest in the lower bole, while no differences were noted between the mid and upper bole heights (Table 2). Conversely, vascular tissue mass was higher in the mid and upper bole versus the lower bole height.

Douglas-fir (77%), Western hemlock (22%), and Sitka spruce (1%; *Picea sitchensis*) were the conifer species identified by the survey of 1,646 trees. Only Douglas-fir and Western hemlock data were subjected

Table 2
Effects of pruning and bole height on vascular tissue chemical constituents.

Response	Treatment	Bole Height
Vascular Tissue Mass	Unpruned>Pruned	Mid=High>Low
Hydrocarbon Monoterpenes	NS[a]	Low>Mid=High
Oxygenated Monoterpenes	NS	Low>Mid=High
Sesquiterpenes	pruned>Unpruned	Low>Mid=High
Total Carbohydrates	Unpruned>Pruned	NS

[a] Not significant at α=0.05.

Table 3
Chi-square results of Douglas-fir damaged by black bears following treatment.

	Bear Damaged: (Observed) (Expected)	No Damage: (Observed) (Expected)
Unpruned:	71	524
	44	551
Pruned:	21	631
	48	604

χ^2=34.6, p<0.00001, Odds=4.07.

Table 4
Chi-square results of Western hemlock damaged by black bears following treatment.

	Bear Damaged: (Observed) (Expected)	No Damage: (Observed) (Expected)
Unpruned:	74	154
	59	169
Pruned:	17	169
	32	94

χ^2=15.3, p=0.00009, Odds=3.08.

to chi-square analyses. Neither Douglas-fir ($\chi^2_{1,1}$ = 0.56, p=0.45) nor Western hemlock ($\chi^2_{1,1}$ = 1.76, p=0.18) were selectively pruned. That is, pruning treatments were applied independently of existing bear damage. Live canopy pruning had a significant impact on bear preference for Douglas-fir (Table 3). The odds ratio suggests that unpruned trees were four times more likely to be damaged than pruned trees at this site. Similarly, unpruned Western hemlock were three times more likely to be damaged than pruned trees (Table 4).

4. Discussion

Live canopy pruning had significant impacts on the growth and chemistry throughout the bole of the tree. Pruning resulted in decreased growth, particularly in the lower bole. We used the mass of vascular tissue in the 800 cm^2 sample area as a measure of current year's growth. Decreased radial growth in the lower bole due to live canopy pruning has previously been demonstrated (Langstrom and Hellqvist, 1991). This effect was still evident two years following radial pruning of the lower portion of the live canopy.

The carbohydrate content of vascular tissue was significantly impacted by live canopy pruning. Growth in the cambial zone is closely tied to the carbohydrate concentration (Kramer and Kozlowski, 1979). Thus, it is not surprising that pruning also resulted in decreased vascular tissue carbohydrate content. However, the observation that pruning did not profoundly effect vascular tissue terpene concentration was unexpected. Plant responses induced by tissue injuries have been widely investigated (see Karban and Meyers, 1989 for review). Changes in the chemical defense of woody plants have been shown to result from herbivore pruning and defoliation (Bryant et al., 1991a). The increase in sesquiterpene concentration may have been an induced response to pruning. However, sesquiterpenes are only a minor constituent of the terpenes present in Douglas-fir vascular tissue (Kimball et al., 1995).

Differences in vascular tissue chemistry may explain why unpruned Douglas-fir were foraged upon by bears more often than pruned trees at the God's Valley site. Vascular tissues of unpruned Douglas-fir had higher carbohydrate concentrations than their pruned neighbors, while the terpene concentration remains unchanged. Diet preferences based on the positive post-ingestive feedbacks of carbohydrates are common in mammals (Sclafani, 1990). Similarly, aversions resulting from the ingestion of toxins have been well established (see Palo and Robbins, 1991). Terpenes are thought to mediate avoidance via a toxic effect (Bryant et al., 1991b). Like other toxins, terpenes can be detoxified. However, detoxification of plant secondary metabolites comes at a metabolic cost to the animal (Illius and Jessop, 1995; Foley et al., 1995).

Our results suggest that when offered a choice, bear selection of unpruned Douglas-fir achieved the desired goal of maximizing carbohydrate intake while not increasing terpene exposure. Selection of unpruned Western hemlock over pruned Western hemlock may also have resulted from differences in the chemical constituents of the vascular tissue.

Mammalian diet selection based on the chemical constituents of the forage item is well known (Cork and Foley, 1991). Animals learn to associate the flavor of a food with the postingestive feedbacks resulting from consumption (Provenza et al., 1992). Furthermore, congnitive processes allow animals to associate visual, tactile, and odor cues to these same feedbacks. Black bear preference for the vascular tissue of unpruned trees over pruned trees may be fostered via these learning processes. In fact, vascular tissue foraging in general may be a learned process.

Maternal learning is a common pathway animals may develop forage preferences (Provenza, 1995). The observation that bear foraging occurs mainly in the lower bole is consistent with the suggestion that vascular tissue foraging is a learned behavior. While bears have learned that vascular tissue is an excellent source of energy, resources available higher in the bole remain largely unused. Chemical data indicate that the carbohydrate content of vascular tissue does not change due to bole height. Furthermore, the terpene concentration is lower in the mid and upper bole. Thus, data suggest that black bears would benefit from choosing to forage higher in the bole of conifers. Foraging activity may be limited to the lower bole, however, because few animals have experienced foraging higher in the bole. Observed damage in the mid and upper bole probably resulted from individual bears that encountered vascular tissue higher in the bole and learned that terpene exposure is further reduced by this behavior.

Our data suggest that live canopy pruning may offer cost effective means to alleviate black bear foraging damage. A recent study estimated the cost of pruning up to 5.5 m to range from $2.34 (U.S.) to $6.42 per tree (O'Hara et al., 1995). Pruning, as applied in this study, can extend protection to specific trees within a stand. On a larger scale, pruning of 50% of trees can influence bear foraging such that complete losses of trees in small localized areas or 'pockets' could be avoided. The efficacy of pruning a higher percentage of the trees in a stand needs further investigation.

Acknowledgements

The authors are particularly grateful for the input of William Voelker on the design of this study and the efforts of John Beck, Jerry Guthrie, and Steve Kendall in the field. Portions of this work were funded by the Collaborative Research Team. The review comments of Dr. Michael Fall, Dr. John Johnston, and Dr. Gary Witmer were greatly appreciated. Mention of specific products does not constitute endorsement by either the United States Department of Agriculture or the Oregon Department of Forestry.

References

Barnes, V.G., Jr., Engeman, R.M., 1995. Black bear damage to lodgepole pine in Central Oregon. Northwest. Nat. 76, 127–129.

Bryant, J.P., Kuropat, P.J., Reichardt, P.B., Clausen, T.P., 1991a. Controls over the allocation of resources by woody plants to chemical antiherbivore defense. In: Palo, R.T., Robbins, C.T. (Eds.), Plant Defenses against mammalian herbivory. CRC Press, Boca Raton, pp. 83–102.

Bryant, J.P., Provenza, F.D., Pastor, J., Reichardt, P.B., Clausen, T.P., du Toit, J.T., 1991b. Interactions between woody plants and browsing mammals mediated by secondary metabolites. Ann. Rev. Ecol. Syst. 22, 431–446.

Cork, S.J., Foley, W.J., 1991. Digestive and metabolic strategies of arboreal mammalian folivores in relation to chemical defenses in temperate and tropical forests. In: Palo, R.T., Robbins, C.T. (Eds.), Plant Defenses against mammalian herbivory. CRC Press, Boca Raton, pp. 133–166.

Foley, W.J., McLean, A., Cork, S.J., 1995. Consequences of biotransformation of plant secondary metabolites on acid–base metabolism in mammals – A final common pathway? J. Chem. Ecol. 21, 721–743.

Illius, A.W., Jessop, N.S., 1995. Modeling metabolic costs of allelochemical ingestion by foraging herbivores. J. Chem. Ecol. 21, 693–719.

Kanaskie, A., Chetock, J., Irwin, G., Overhulser, D., 1990. Black bear damage to forest trees in Northwest Oregon 1988–1989, Pest Management Report 90-1, Oregon Department of Forestry, Salem, OR.

Karban, R., Meyers, J.H., 1989. Induced plant responses to herbivory. Ann. Rev. Ecol. System 20, 331–348.

Kimball, B.A., Craver, R.K., Johnston, J.J., Nolte, D.L., 1995. Quantitative analysis of the mono- and sesquiterpenoids of Douglas-fir vascular tissue by solvent extraction and gas chromatography with mass selective detection. J. High Resol. Chromatogr. 18, 221–225.

Kimball, B.A., Nolte, D.L., Engeman, R.M., Johnston, J.J., Stermitz. F.R., Chemically mediated foraging preference of black bears (Ursus americanus). J. Mammal. (in press).

Kramer, P.J., Kozlowski, T.T., 1979. Physiology of Woody Plants. Academic Press, NY, p. 811.

Langstrom, B., Hellqvist, C., 1991. Effects of different pruning regimes on growth and sapwood area of Scots pine. For Ecol. Manage. 44, 239–254.

Mason, A.C., Adams, D.L., 1989. Black bear damage to thinned timber stands in Northwest Montana. West. J. Appl. For. 4, 10–13.

O'Hara, K.L., 1991. A biological justification for pruning in coastal Douglas-fir stands. West. J. Appl. For. 6, 59–63.

O'Hara, K.L., Larvik, D.A., Valappil, N.I., 1995. Pruning costs for four Northern Rocky Mountain species with three equipment combinations. West. J. Appl. For. 10, 59–65.

Ott, L., 1993. An introduction to statistical methods and data analysis. Duxbury Press, Belmont, CA, USA. p. 818 .

Palo, R.T., Robbins, C.T., 1991. Plant Defenses against mammalian herbivory. CRC Press, Boca Raton, FL, p. 192.

Provenza, F.D., 1995. Tracking variable environments: There is more than one kind of memory. J. Chem. Ecol. 21, 911–923.

Provenza, F.D., Pfister, J.A., Cheney, C.D., 1992. Mechanisms of learning in diet selection with reference to phytotoxicosis in herbivores. J. Range Manage. 45, 36–45.

Rocklin, R.D., Pohl, C.A., 1983. Determination of carbohydrates by anion exchange chromatography with pulsed amperometric detection. J. Liq. Chromatogr. 6, 1577–1590.

SAS, 1990. SAS/STAT Users Guide, Version 6, SAS Institute Inc. Cary, NC.

SMC, 1997. The newsletter of the Stand Management Cooperative, Spring 1997. College of Forest Resources, University of Washington, Seattle, WA, USA.

Schmidt, W.C., Gourley, M., 1992. Chap. 15: Black bear. In: Black, H.C. (Ed.), Silvicultural approaches to animal damage management in pacific northwest forests. USDA Technical Report PNW-GTR-287, pp. 309–331.

Sclafani, A., 1990. Nutritionally based learned flavor preferences in rats. In: Capaldi, E.D., Powley, T.L. (Eds.), Taste, experience, and feeding. American Psychological Association, Washington, D.C., pp. 139–156.